

Reproductive and dietary biology of *Nephrurus* and *Underwoodisaurus* (Gekkonidae) in Western Australia

R.A. How, J. Dell and B.D. Wellington*

Abstract

Six species of *Nephrurus* and *Underwoodisaurus milii* are found in Western Australia and adjacent areas of adjoining states. Dissection of 1163 specimens of the seven species provided data on size and maturity, sex dimorphism, seasonal reproductive pattern and diet. Adult females were larger than adult males in all seven species, however, in *Nephrurus* spp this difference (around 20 percent) was the largest recorded in geckos. Sexual maturity in male *Nephrurus* spp was attained at between 82-89 percent of the size of females at maturity, and at 92 percent in *U. milii*. Sex ratio amongst adults was near parity. Vitellogenesis and spermatogenesis in *Nephrurus* spp can probably occur in any month under favourable environmental conditions, but in *U. milii* male gonads increase in size over winter and vitellogenesis, ovulation and oviposition are focussed in spring and summer. Sequential clutches were recorded for all species. Diet is primarily arthropods but some larger *Nephrurus* spp eat smaller geckos. Species occupying sandy substrates have the most similar diets.

Introduction

Reproductive cycles in Australian reptiles show a diverse array of patterns (Heatwole and Taylor 1987). However, as is common in many reviews of reptile reproduction and population dynamics geckos have received little attention, due principally to their invariable clutch size of either one or two eggs (Ballinger 1983; Fitch 1970).

In Western Australia there are 58 species of geckos occurring in all climatic and vegetation associations from the humid tropics, through the arid and semi-arid centre of the state to the mesic south-west (Storr, Smith & Johnstone 1989). The knob-tailed gecko genus, *Nephrurus*, occurs in a wide variety of habitats from the northern tropics to the semi-arid southwest. The closely related *Underwoodisaurus milii* is distributed across temperate southern Australia and adjacent islands.

In this paper we examine the diet, reproductive pattern, size, sex-ratio and maturity of these species and compare this with published data on congeners and confamilials.

The largest species is *N. asper* which is distributed widely in the Kimberley of northern Western Australia, across the Northern Territory and into western and northern Queensland. It is found on heavy loam soils which have numerous rocks under which it lives. *Nephrurus laevis* occurs on sandy ridges and dunes throughout much of arid eastern Western Australia, southwestern Northern Territory and northwestern South Australia. The arid sandplain specialist *N. levis* is distributed over most of Western Australia except for the Kimberley and southwestern quarter; it is also found in the south of the Northern Territory and the adjacent corners of Queensland and New South

*Department of Terrestrial Vertebrates Western Australian Museum, Perth.

Wales. The semi-arid sandplains of southern Western Australia and western South Australia are occupied by *N. stellatus*. The endemic Western Australian species *N. vertebralis* is found on the heavier loamy soils of the western interior and is often associated with mulga, *Acacia aneura*. *Nephurus wheeleri* is also endemic to Western Australia, also prefers heavy loams, but is generally distributed north of *N. vertebralis* in the Pilbara and upper Murchison regions. The mainly rock-inhabiting *Underwoodisaurus milii* is distributed over much of southern Australia, but in Western Australia is restricted to the region dominated by winter rainfall, except for the extreme south west. The distribution encompasses the islands of the Houtman Abrolhos, West Coast and Recherche Arcipelago. All species are terrestrial and nocturnal.

Methods

This study is based on examination of 1163 specimens from the collections of the Western Australian, South Australian and Northern Territory Museums. A total of 70 *Nephurus asper*, 199 *N. laevis*, 263 *N. levis*, 77 *N. stellatus*, 40 *N. vertebralis*, 50 *N. wheeleri* and 464 *Underwoodisaurus milii* were examined that had been collected opportunistically over the last 60-70 years.

Snout-vent length (SVL) was measured on all specimens. Mid-ventral and lateral incisions were then made to examine reproductive tracts. Maximum length and width of testes, ovarian follicles, and oviducal eggs were measured by one of us (BDW) using dial vernier calipers to the nearest 0.1 mm.

Stomach contents were removed and sorted into major prey categories. Plant material, sand, feathers (presumably ingested accidentally), and parasitic nematodes were not considered as part of the diet in calculations of dietary breadth and overlap. Prey categories conform approximately with those of Pianka and Pianka (1976).

Females were judged as adult by the presence of thickened or convoluted oviducts and/or the presence of enlarged yolked follicles or eggs; reproductively active females were those with yolky follicles, eggs or both. Females with oviducts previously removed were excluded from analysis. Males showed considerable variation in testicular size but were deemed adult by expanded efferent ducts and enlarged testes. Reproductive information was assessed by month regardless of year of collection.

The volume of testes, follicles or eggs was estimated to the nearest 0.1 mm using the equation for a prolate spheroid (Selby, 1965): $V = 4/3 (l/2)(w/2)^2$ where l is length and w is width. Calculation of dietary breadth followed the method of Pianka and Pianka (1976)

$$B = \frac{1}{n \sum_{i=1}^n p_i^2}$$

where p_i is the proportion (by number) of the i th resource and n the number of resource categories.

Dietary overlap is

$$O_{jk} = \frac{\sum_{i=1}^n P_{ij} P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}},$$

where n is the number of resource states and p_{ij} and p_{ik} are the proportions (by numbers) of the i th resource used by the j th and k th species respectively.

Data are summarized as mean, standard deviation, and sample size. Where appropriate, data were submitted to a least squares regression analysis.

Results

Body Size and Sex Ratio

The body size of adults showed significant sexual dimorphism in all species examined (Table 1). Within the genus *Nephrurus* females were almost 20 percent larger than males in all species. Female *Underwoodisaurus* were only slightly larger than males.

Table 1: Mean and maximum snout-vent lengths (SVL), size ratio and sex ratio of six adult *Nephrurus* species and *Underwoodisaurus*, and the number of sub-adults and juveniles examined. (***) = $P < 0.001$ for male and female SVL comparison).

Species	Adult				Preadults						
	♂♂SVL				♀♀SVL				♂♀ Sex		
	x	SD	n	max	x	SD	n	max	SVL	Ratio	n
<i>N. asper</i>	84.9	11.0	24	102.5	98.5***	12.2	28	113.1	1.16	0.46	18
<i>N. laevis</i>	66.4	5.6	78	77.8	77.0***	6.1	71	90.1	1.16	0.52	50
<i>N. levis</i>	69.9	4.6	65	85.5	82.8***	6.9	73	98.3	1.18	0.47	125
<i>N. stellatus</i>	68.4	5.9	27	80.6	80.4***	6.0	14	90.6	1.18	0.66	36
<i>N. vertebralis</i>	64.5	6.8	17	74.2	79.6***	9.1	10	90.0	1.23	0.63	13
<i>N. wheeleri</i>	76.3	4.0	17	86.8	90.0***	6.2	18	100.4	1.18	0.49	25
<i>U. milli</i>	77.1	7.4	175	91.8	80.3***	7.6	153	96.5	1.04	0.53	136

Examination of intraspecific size variation was made by comparing the 3 subspecies of *N. levis*, the Kimberley and Northern Territory specimens of *N. asper* and island and mainland specimens of *U. milli*.

Male *N. l. levis* SVL (mm) (71.8 ± 2.9 (17)) were significantly ($t_{56} = 4.3$ $P < .001$) larger than *N. l. occidentalis* (68.2 ± 3.7 (41)) but not significantly larger than *N. l. pilbara* (74.9 ± 7.1 (7)); males of the latter 2 subspecies did not differ significantly. Female *N. l. levis* (85.7 ± 5.9 (19)), *N. l. pilbara* (82.8 ± 7.5 (6)) and *N. l. occidentalis* (81.7 ± 7.0 (48)) did not differ significantly from one another.

Northern Territory males and females of *N. asper* had SVL's of 86.9 ± 12.9 (11) and 106.4 ± 8.2 (10) respectively, compared with 84.7 ± 8.1 (13) and 91.9 ± 11.3 (18) for Kimberley males and females. Kimberley adult females are significantly ($P < .001$) smaller than those in the Northern Territory, but males did not differ between the regions.

Mainland *U. milii* males (76.0 ± 7.4 (127)) are significantly ($t_{173} = 3.06$ $P < 0.01$) smaller than island males (79.9 ± 6.4 (48)). Size of females did not differ significantly between mainland (80.0 ± 8.1 (100)) and island (81.0 ± 6.5 (53)) populations.

The adult sex ratio was close to parity in all species except *N. stellatus* and *N. vertebralis* where a greater proportion of males was examined.

Maturity and Reproductive Activity

Examination of the reproductive tracts of both sexes, as described in Methods, allowed a determination of the size at onset of maturity in these gecko species. These data are presented in Table 2.

Nephrurus males become reproductively adult at between 82-89% of the size at which females are first observed with follicles or convoluted oviducts. In *U. milii*, males were about 92% the size of females at reproductive maturity (Table 2).

Table 2: Size of gravid and adult *Nephrurus* species and *Underwoodisaurus* and the maximum and mean clutch volumes and sexual dimorphism at maturity.

	<i>Nephrurus</i>						<i>U.</i>
	<i>asper</i>	<i>laevisissimus</i>	<i>levis</i>	<i>stellatus</i>	<i>vertebralis</i>	<i>wheeleri</i>	<i>milii</i>
FEMALES							
Largest gravid (SVL)	113.1	90.1	95.8	90.6	90.0	94.6	96.5
Smallest gravid (SVL)	90.0	70.8	71.0	84.0	67.3	82.3	65.2
Smallest adult (SVL)	73.0	64.9	71.0	70.5	66.7	80.5	64.2
Mean gravid size (SVL)	100.4	78.1	83.9	87.2	84.1	88.9	83.4
Mean gravid size SD (n)	8.5(8)	6.5(8)	6.6(32)	3.3(3)	9.5(5)	4.7(7)	9.5(18)
Mean clutch volume (mm ³)	4637	2543	3383	3611	1540	3547	2154
Mean clutch volume SD (n)	2107(8)	782(8)	1499(33)	1048(3)	1000(5)	1719(8)	516(16)
Max clutch volume (mm ³)	7234	3902	7423	4766	2838	5597	3245
MALES							
Size at maturity (SVL)	65	55	62	59	55	70	59
♂:♀ mature SVL (%)	89.0	84.7	87.3	83.7	82.5	87.0	91.9

The smallest individual recorded and the month of capture were (SVL; mm): *N. asper* - 42.0, May; *N. laevisissimus* - 31.2, March; *N. levis* - 33.0, August; *N. stellatus* - 40.2, April; *N. vertebralis* - 37.1, March; *N. wheeleri* - 37.5, June and *U. milii* - 30.4, June.

The annual variation in mean monthly testicular volume of adult males is presented in Figure 2 and contrasted with the reproductive activity of adult females (Figure 1).

In most *Nephrurus* species the number of adult males collected during any month is low, and the variation in mean testicular volume high. This suggests that some males of all species may be reproductively active each month or that testis volume is not strongly

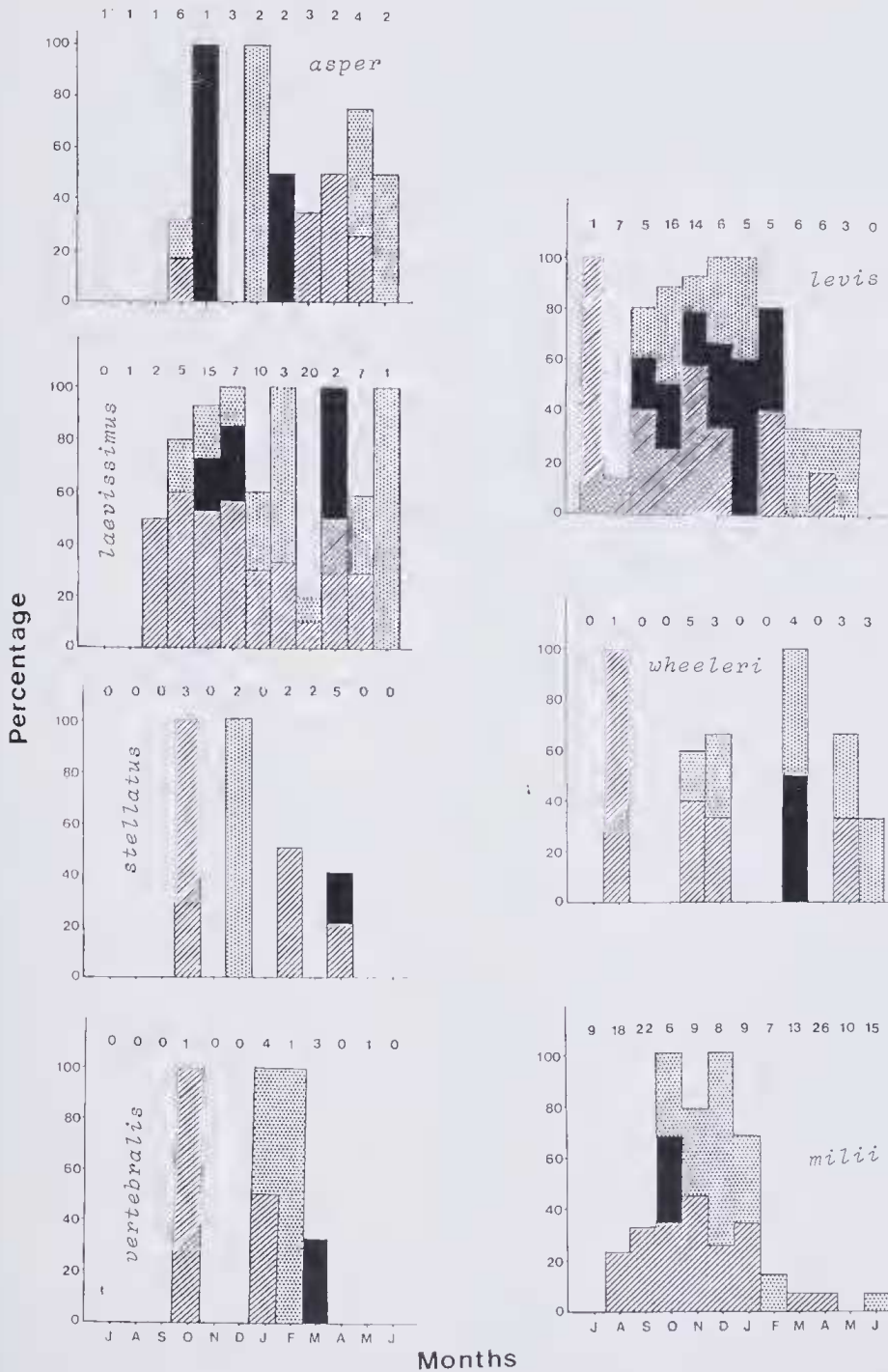


Figure 1: Percentages of reproductively active *Nephurus* spp. and *U. milii* females apportioned according to yolky follicles (cross hatching), eggs (stippling) or both (blocked). Numbers of adults examined for each month is given.

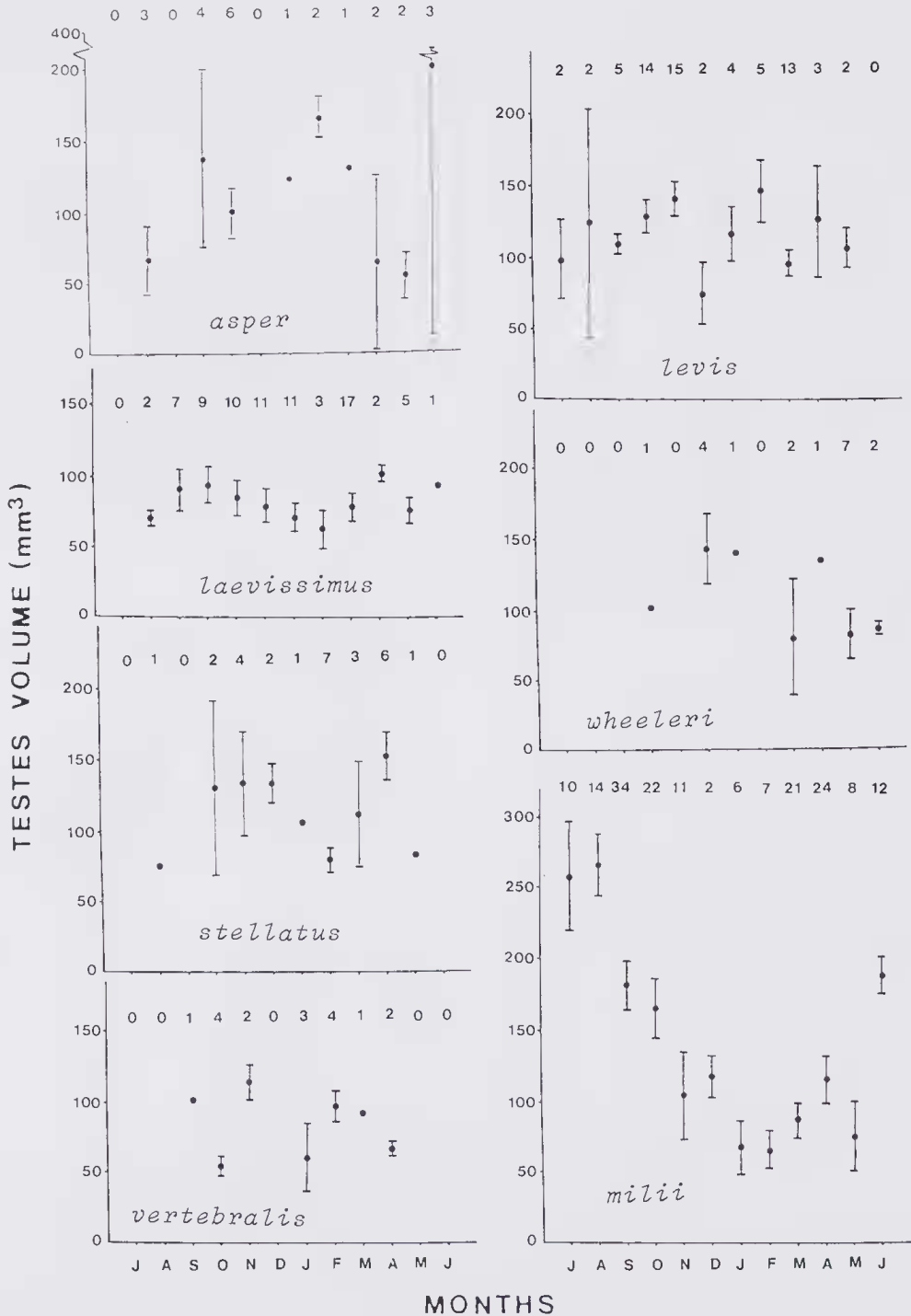


Figure 2: Variation in testes volume (mm³) of *Nephurus* spp. and *U. mii*. Data are presented as means \pm 1 SE (n).

correlated with reproductive activity — alternatives that can only be resolved by histological examination. Female numbers are similarly low and reproductive activity was recorded in nearly every month where sample sizes were greater than one. Females appear to breed throughout the year, and some females in each species possess both eggs and yolky follicles, indicating that repetitive clutching can occur. Small sample sizes prevented evaluation of reproductive patterns in the three subspecies of *N. levis* and the geographic populations of *N. asper*.

Clutches of a single egg were recorded in *N. asper* (1), *N. levis* (1), *N. stellatus* (1), *N. vertebralis* (1) and *U. milii* (2), but in all cases a distended contralateral oviduct suggested recent laying of an egg from that side.

Gonad volumes in male *U. milii* are markedly higher during winter and early spring than those recorded during other months (Figure 2). Testicular volumes are generally greater than those recorded in *Nephrurus* spp. Female *U. milii* have a distinct breeding season, with eggs generally being recorded between October and January. There is a unique instance of a gravid female in June (Figure 1). Two females collected in October had both yolky follicles and eggs, suggesting that some double clutches may occur in this species. We were unable to find any differences in the reproductive pattern of this species in island and mainland populations.

There is a significant relationship within the *Nephrurus* genus between mean size of gravid females and mean clutch volume. $\text{Vol (mm}^3\text{)} = 107.30 \text{ SVL} - 6135.80$ ($r = 0.76$ $P < 0.05$)

Diet

The stomach contents of six species, identified to ordinal level, are presented in Table 3. These data may underestimate the quantity of soft-bodied invertebrates in the diet which are digested rapidly, but they are comparative with other studies of stomach contents.

Arthropods formed the principal dietary items of all species. The occurrence of lizards in the stomachs of *N. levis* and *U. milii* suggests that both of these larger species may occasionally ingest other members of the saurofauna. The euryphagous habit of species is exemplified by the relatively large dietary breadths of all species examined.

Dietary overlap (Table 4) is almost always in excess of 0.700, reaching a maximum of 0.920 between *N. levis* and *N. laevis*. The mean overlap within the genus *Nephrurus* is 0.806 ± 0.085 (10) while between *U. milii* and the 5 *Nephrurus* species it is 0.705 ± 0.055 (5).

Discussion

The sexual size dimorphism in *Nephrurus* is the largest recorded in the family Gekkonidae. Fitch (1981) documented female to male size differences of between 84 and 115% in the 43 species of geckos he surveyed. In *Nephrurus* the size differences range from 116% to 123% (Table 1). *Underwoodisaurus milii* also has larger females, but the size dimorphism is within the range for the family described by Fitch (1981).

Table 3: Number of stomachs in which different prey categories occurred, the number of stomachs examined and the dietary breadth of *Nephrurus* spp. and *Underwoodisaurus*.

<i>asper</i>	<i>Nephrurus</i>				<i>Underwoodisaurus</i>	
	<i>laevissimus</i>	<i>levis</i>	<i>stellatus</i>	<i>vertebralis</i>	<i>wheeleri</i>	<i>mili</i>
Isopods		5		1	1	24
Centipedes	10	25	3	1	2	12
Scorpions	10	16	4	4	2	8
Spiders	15	34	4	4	8	57
Thysanura 1						
Formicoidea	2	5	1	1		5
Other Hymenoptera						7
Orthoptera	7	18	1	6	5	19
Blattodea	11	16	5	4	1	43
Mantids/ Phasmids	1					
Curculionoidae	5	1		1		13
Other Coleoptera	12	18	3		1	28
Isoptera	2	2				2
Dermoptera		6				20
Diptera	1					2
Lepidoptera	1					5
Odonata	2					
Eggs	3	5		2		13
Larvae/ Pupae	4	2	2		1	55
Winged insects	6			2	1	3
Unidentified insects	2	2		1	1	36
Lizards and Sloughs		4				1
Plant material	1	2				6
Bone	1			1		
Sand	6	20	2	2		5
Unidentified material	5	2	4	3	1	
Nematodes	20	19		3	3	14
Stomachs with food	59	95	16	21	18	192
Stomachs examined	105	265	83	40	63	594
Dietary Breadth	0.590	0.519	0.816	0.693	0.514	0.537

Table 4: Dietary niche overlap in five *Nephrurus* species and *Underwoodisaurus mili* based on numerical frequency of occurrence.

	<i>laevissimus</i>	<i>levis</i>	<i>stellatus</i>	<i>vertebralis</i>	<i>wheeleri</i>	<i>U. mili</i>
<i>laevissimus</i>	1					
<i>levis</i>	0.920	1				
<i>stellatus</i>	0.910	0.873	1			
<i>vertebralis</i>	0.779	0.768	0.699	1		
<i>wheeleri</i>	0.780	0.864	0.668	0.800	1	
<i>U. mili</i>	0.758	0.723	0.733	0.614	0.696	1

Correlations of larger female size in reptiles with both viviparous reproduction and large mean number of offspring each reproduction as noted by Fitch (1981) do not apply to geckos (How, Dell & Wellington 1986). However, positive correlates with both occupancy of temperate regions and small body size were also noted by Fitch (1981) and these can be assessed from the present data. There is no indication within the genus *Nephrurus* that species in more temperate areas (*stellatus*) show any greater size dimorphism than those in tropical (*asper*) or arid (*vertebralis*) areas. The smallest species, *N. vertebralis*, had the greatest size dimorphism, but another small species, *N. laevis*, showed the least.

Male *Nephrurus* are reproductively adult at between 82-89% of the size of females at the same stage and mean size of all adult males is between 81-86% of mean adult female size. There is no data on growth rates in *Nephrurus*, so it is not possible to determine if males reach maturity at the same age as females but have a slower growth or whether maturity is reached at an earlier age. However, since both mean adult size and size at maturity is less in males it is possible that growth rates are slower in this sex. In *Oedura reticulata* in southwestern Australia males and females have similar growth rates, but males mature a year earlier i.e. at a smaller body size (How & Kitchener 1983). The findings of Dunham (1978) on the correlation between food abundance and growth rates should limit speculation on these parameters for geckos living in highly variable environments.

Our finding of male maturity in *Nephrurus* occurring at between 82-89% of female size (Table 2) is in agreement with the generalisations of Stamps (1983) of between 83-92% for geckos. It differs, however, from our earlier studies on members of the *Strophurus* group of geckos (How, Dell & Wellington 1986) where male maturity occurred between 94-100% of female size.

Fewer *Nephrurus* individuals have been collected during winter months and sample sizes during this season were invariably low. It is probable that this reflects a real decrease in activity during these months since nocturnal temperatures in arid environments of central Australia often approach and/or drop below freezing. Pianka and Pianka (1976) showed marked seasonal changes in activity patterns of twelve species of geckos occupying the arid zone. In a study of *Oedura* and *Gehyra* in semi-arid Western Australia, Kitchener, How & Dell (1988) showed a decrease in activity below 16-18° C with a virtual cessation of activity below 12° C. Our data also indicate decreased activity amongst *Nephrurus* in summer and autumn, however, this probably reflects decreased collecting activity during these very hot months. Specimens of *U. milii* show a bimodal peak in abundance (Figure 1 & 2) for both spring and autumn periods in both sexes.

The recent review of reproductive ecology of Australian reptiles by Heatwole & Taylor (1987) has documented eleven basic types of cycles.

The reproductive pattern of female *U. milii* is that of spring vitellogenesis with ovulation and oviposition during late spring and early summer. This pattern has been characterised for several temperature zone south-western geckos (How & Kitchener 1983, How, Dell & Wellington 1986, How, Dell & Gordon 1987) where species occupying winter-rainfall areas produce clutches in spring and summer with hatchlings

first appearing in early autumn. Male *U. milii* have greatest testicular volumes in winter and early spring (Figure 2), around 3-4 months earlier than the onset of vitellogenesis. If spermatogenesis is associated with maximum gonad volume and mating occurs at the time of maximum gonadal activity, then sperm storage must occur in this species for fertilisation to occur. This pattern would suggest that *U. milii* has a reproductive cycle of the Type IX of Heatwole & Taylor (1987), and contrasts to the Type I and II pattern recorded for other geckos (Bustard 1968, King 1977, How, Dell & Gordon 1987, Kitchener, How & Dell 1988).

Reproductive patterns in *Nephrurus* suggest that activity may occur throughout the year. This is not uncharacteristic of arid zone species where environmental conditions may be favourable for short periods after rain at almost any time of the year. However, the greatest activity still occurs in the warm-hot months of spring and summer. *Nephrurus asper*, with its distribution focussed on the wet-dry tropics, shows that reproductive activity extends over at least nine months — spanning the October-April wet period — a pattern consistent with Type VIII of Heatwole and Taylor (1987). The small number of individuals collected during the cooler winter months prevents an accurate classification of reproductive pattern in the remaining *Nephrurus* species.

In all species some individuals had both oviducal eggs and developing yolky ovarian follicles, indicative that repetitive clutches are produced. This condition has also been recorded in several *Strophurus* species (How, Dell & Wellington 1986), *Gehyra variegata* (Kitchener, How & Dell 1988) and *Phyllodactylus marmoratus* (How, Dell & Gordon 1987) in Western Australia and could be a widespread phenomenon in Australian geckos.

Previous studies have documented clutch volumes (mm^3) for *N. laevis* (2160: Pianka & Pianka, 1976), *N. levis* (3260: Pianka & Pianka 1976) and *N. deleani* (4077: Delean & Harvey, 1984, Harvey 1983). Our data confirm that *Nephrurus* have large clutch volumes and that larger species have larger volumes. A similar relationship was recorded in *Strophurus* (How, Dell & Wellington 1986).

The diet of *N. laevis*, *N. levis* and *N. vertebralis* has been documented previously from an analysis of stomach contents. These species eat large numbers of arthropods, especially spiders, beetles and locusts, with occasional lizards and sloughed skins recorded in *N. laevis* and *N. vertebralis* stomachs (Pianka & Pianka 1976). The gecko *Rynchoedura ornata* was eaten by all three *Nephrurus* species and *N. vertebralis* also ate the gecko *Diplodactylus conspicillatus*. Their study also showed a low dietary niche overlap between *N. vertebralis* and *N. laevis* (0.42) and *N. levis* (0.53), but a relatively high overlap between *N. laevis* and *N. levis* (0.82). Our comparative figures for these species pairs are 0.78, 0.77 and 0.92 respectively (Table 4), and also indicate a higher dietary overlap between the latter pair. Diets determined by Pianka and Pianka (1976) were from individuals collected at the same sites at similar times. It is interesting to note that Museum specimens, collected from many different sites over many years, show similar dietary patterns and overlaps. Because both *N. levis* (a sandplain specialist) and *N. laevis* (a sand dune specialist) prefer sandy habitats it is probable that the arthropod fauna of these substrates is more similar than that of the

harder loamy soils frequented by *N. vertebralis*. High overlap also occurs between *N. stellatus* and the other two *Nephrurus* that prefer sandy soils.

References

- Ballinger, R.E. 1983. Life history variations. Pp. 241-260. In R.B. Huey, E.R. Pianka, and T.W. Schoener (Eds.), *Lizard Ecology*. Harvard University Press, Cambridge, Massachusetts.
- Bustard, H.R. 1968. The ecology of the Australian gecko, *Gehyra variegata* in northern New South Wales. *J. Zool. (Lond.)* **156**: 483-497.
- Delean, S. & C. Harvey, 1984. Notes on the reproduction of *Nephrurus deleani* (Reptilia: Gekkonidae). *Trans. R. Soc. S. Aust.* **108** (4): 221-222.
- Dunham, A.E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* **59**: 770-778.
- Fitch, H.S. 1970. Reproductive cycles of lizards and snakes. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 52.
- Fitch, H.S. 1981. Sexual size differences in reptiles. *Univ. Kansas Mus. Nat. Hist. Misc. Publ.* 70.
- Harvey, C. 1983. A new species of *Nephrurus* (Reptilia: Gekkonidae) from South Australia. *Trans. R. Soc. S. Aust.* **107** (4): 231-235.
- Heatwole, H. and J. Taylor. 1987. *Ecology of Reptiles*, Surrey Beatty & Sons, Chipping Norton.
- How, R.A. and D.J. Kitchener. 1983. The biology of the gecko *Oedura reticulata* Bustard, in a small habitat isolate in the Western Australian wheatbelt. *Aust. Wildl. Res.* **10**: 543-556.
- How, R.A., J. Dell and S.J. Gordon. 1987. Reproductive patterns in chromosomally distinct races of *Phyllodactylus marmoratus* (Lacertilia: Gekkonida) in South-western Australia. *Rec. West. Aust. Mus.* **13**: 413-418.
- How, R.A., J. Dell, and B.D. Wellington. 1986. Comparative biology of eight species of *Diplodactylus* gecko in Western Australia. *Herpetologica* **42**: 471-482.
- King, M. 1977. Reproduction in the Australian gekko *Phyllodactylus marmoratus* (Gray). *Herpetologica* **33**: 7-13.
- Kitchener, D.J., R.A. How and J. Dell. 1988. Biology of *Oedura reticulata* and *Gehyra variegata* (Gekkonidae) in an isolated woodland of Western Australia. *J. Herpet.* **22**: 401-12.
- Pianka, E.R. and H.D. Pianka. 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* **1976**: 125-142.
- Selby, S.M. 1965. *Standard Math Tables*, 14th Ed. Chemical Rubber Co., Cleveland.
- Stamps, J.A. 1983. Sexual selection, sexual dimorphism, and territoriality. Pp. 169-204. In R.B. Huey, E.R. Pianka, and T.W. Schoener (Eds.), *Lizard Ecology*. Harvard University Press, Cambridge, Massachusetts.
- Storr, G.M., L.A. Smith and R.E. Johnstone. 1990. *Lizards of Western Australia III Geckos and Legless Lizards*. W.A. Museum.